Vegetation structure, phenology, and regeneration in the natural and anthropogenic tree-fall gaps of a reduced-impact logged subtropical Bolivian forest

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Abstract

Reduced-impact logging is a type of selective logging that incorporates a variety of techniques aimed at lowering levels of damage to the residual stand. In a Bolivian subtropical humid forest we studied differences in gap size, vegetation structure, regeneration and phenology between anthropogenic and natural gaps in a reduced-impact logged and unlogged forest. Harvesting took place between 1 and 4 years previously. Logging gaps were significantly larger than natural gaps (d.f. 1, variance ratio (vr.) 6.38, $p = 0.014$) and had significantly lower coverage of lianas (d.f. 1, vr. 8.64, $p < 0.01$). Seedlings were more prevalent in logging gaps than in natural tree-fall gaps (d.f. 1, vr. 13.97, $p < 0.001$), as were members of the herbaceous genus *Heliconia* (d.f. 4, vr. 3.05, $p = 0.023$). In larger gaps microclimatic conditions favour the regeneration of non-commercial pioneer species. We propose that ground disturbance during bole removal causes higher rates of mortality to shade-tolerant species in advanced stages of regeneration. This removes the competitive height advantage needed by shade-tolerant species to compete within gaps, and thus further promotes the opportunity for pioneer species to dominate gap regeneration. These observed differences between anthropogenic and natural tree-fall gaps are of direct importance to forest managers attempting to understand how disturbance associated with reduced-impact logging influences the regeneration of commercial tree species in Bolivian forestry concessions. We discuss the ecological and silvicultural implications of these results.
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1. Introduction

Disturbance is fundamental to the development, structure, and composition of forest ecosystems (Attiwill, 1994), and can be defined as a ''rapid release or reallocation of community resources'' (Sheil and Burslem, 2003). Disturbance varies spatially and temporally in forests from frequent low intensity gap-forming disturbances operating at the scale of individual trees, to infrequent landscape scale high intensity events (e.g. fires, severe storms) that can significantly alter entire stands (Coates and Burton, 1997). Tree falls, and the gaps they create, represent a source of numerous relatively small scale autogenic disturbances within a forest that are simultaneously a source of mortality for some individual plant species and an opportunity for establishment for others (Denslow, 1980).

The species which eventually establish within a particular gap are determined both by niche partitioning and stochastic processes (Brokaw and Busing, 2000; Schnitzer and Carson, 2000). A fundamental axis of niche partitioning among tropical tree species is their regeneration strategy (Grubb, 1977; Pacala et al., 1996), and although the regeneration strategies of different tropical trees are best represented by a continuum (Wright et al., 2003), it remains useful to distinguish the two broad niche categories of ''shade-tolerant'' (primary) or ''shade-intolerant'' (pioneer) species (Hartshorn, 1980). Shade-tolerant species are capable of germinating in the closed forest understorey where root competition is often intense, and can exist in a suppressed juvenile state for some time until improved light conditions permit further growth. In contrast, shade-intolerant species almost exclusively germinate in gaps from seed, where light levels are high and root competition is reduced (Brokaw, 1985).

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Denslow (1980) proposed that, within a given forest community, there is a coupling between the relative commonness of different disturbance-related regeneration strategies, and the frequency of associated disturbance-derived regeneration sites. Empirical evidence supports this view that specific attributes of a given disturbance site influences the composition of the plant community that eventuates (Brokaw, 1985). For example, the size of a gap influences the duration and intensity of light received (Lee, 1978) and there is often a threshold size of gap below which pioneer species are not found (Hartshorn, 1978; Foster and Brokaw, 1982).

Although regeneration strategies are important determinants of gap partitioning by different plant species, stochastic processes, such as pre-gap advanced regeneration, can both limit the degree to which partitioning occurs and increase species diversity in gaps (Brokaw and Scheiner, 1989; Brokaw and Busing, 2000).

The association between disturbance processes and the resulting plant community (Denslow, 1980) is of direct relevance to forest managers trying to ensure that selective logging is ecologically and silviculturally sustainable. With a significant proportion of the world's forests used for timber production, and growing concern for the fate of forest biodiversity (Lindenmayer and Franklin, 2002), there have been calls for forest management to be as consistent as possible with natural disturbance processes (Lindenmayer and McCarthy, 2002; Messier and Kneeshaw, 2003). The further that anthropogenically created disturbances diverge from their natural counterparts, the more likely that stand recovery following selective logging will take a trajectory different from that supportive of the original complement of forest biodiversity. Forest managers are therefore directly responsible for the creation of conditions that will either favour or hinder the regeneration needs of both ecologically and silviculturally important tree species (Lindenmayer and Franklin, 2002).

Nearly 50% of lowland Bolivia is covered by subtropical and tropical forests (Pacheco, 1998), with almost half of these areas granted to timber concessions (Mostacedo and Fredericksen, 1999). In 1996, a new forestry law was enacted to promote the sustainable harvesting of timber (Mostacedo and Fredericksen, 1999). To achieve best-management practices, reduced-impact logging techniques have gained widespread application in Bolivia and, as of 2005, concessions covering over 2.2 million ha had obtained certification by the Forest Stewardship Council.

Reduced-impact logging incorporates a variety of techniques aimed at lowering levels of damage to the residual stand. These include directional felling, pre-harvest vine cutting, and preliminary inventories to reduce the number and density of logging roads (Heinrich, 1995). Recent studies suggest that reduced-impact logging of tropical forests causes less damage to forest structure than conventional selective logging techniques (Asner et al., 2004a; Huth et al., 2004). Although RIL techniques potentially bring disturbance levels closer to natural disturbance regimes, there remains concern both from ecologists and forest managers regarding how RIL-induced changes to forest structure are likely to affect the ecological and silvicultural sustainability of harvested forests over future decades (Lugo, 1999; Bojanic and Bulte, 2002; Dauber et al., 2005).

We suggest that in keeping with goals to improve both timber and non-timber management of tropical forests in Bolivia, there is a need to assess: (1) short-term differences in the vegetation structure and phenology of anthropogenic gaps and natural tree-fall gaps in reduced-impact logged and unlogged forests, and (2) how these differences can affect ecological and silvicultural sustainability. In this paper, we use a reduced-impact logged lowland tropical forest in Santa Cruz province, Bolivia, as a case study to examine differences between logging gaps and natural tree-fall gaps in (i) vegetation structure and phenology; (ii) density and composition of understorey regeneration; and (iii) to assess the potential silvicultural and ecological repercussions of differences between anthropogenic and natural disturbance processes.

2. Methods

2.1. Site description

Our study area was located in the lowland subtropical humid forest (Holdridge Life Zone System) of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia. Research was conducted in the 100,000 ha forestry concession "La Chonta". This is owned and managed by Agroindustria Forestal La Chonta (509,000 to 545,000 easting, 8,275,500 to 824,900 northing, Fig. 1). The forest varies in altitude from 230 to 390 m with an average elevation of 320 m. The area is a continuation of the Brazilian Shield with low fertility soils consisting of oxisols, ultisols, and inceptisols (Park et al., 2005). The mean

Fig. 1. Map of Bolivia with approximate location of the La Chonta forestry concession indicated within the province of Santa Cruz.

annual temperature is 25 °C with a mean annual precipitation of approximately 1560 mm. The region experiences a distinct dry season from May to October during which time cold fronts can reduce temperatures to 5 °C. The forest was bordered by palm savanna to the east with the southern boundary delimited by the Rio Blanco. Forest formerly occurred to the north and west of the concession, but has been extensively cleared for agriculture. Historically, the entire concession was subjected to both legal and illegal selective logging of Mahogany (*Swietenia macrophylla* King), Spanish Cedar (*Cedrela odorata* L.), and a few other highly valuable species 10–25 years prior to this study. The concession was certified by SmartWood in 1998, an independent third-party certifier endorsed by the Forest Stewardship Council.

2.2. Harvesting procedure

Between 60 and 70% of the concession is considered to have sufficient densities of timber to be commercially harvestable (Gil, 1997). Approximately 2500 ha is harvested annually over three contiguous 850 ha blocks (∼4 km × 2 km), yielding 50,000 m^3 of timber product. Eighteen commercial tree species were harvested during the time of this study (2003–2004) including *Ficus boliviana* Berg, *Hura crepitans* L., *Terminalia oblonga* Ruiz & Pavón, *Pseudolmedia laevis* Ruiz & Pavón, *Cariniana ianeirensis* Knuth, and *C. estrellensis* Raddi. Average harvest intensity was approximately 4 trees/ha (Jackson et al., 2002).

The forestry company La Chonta conducts an inventory of harvestable trees 1 year prior to logging. The minimum size for harvest is 50 cm diameter at breast-height (dbh) for all species except *F. boliviensis* and *H. crepitans*, which are harvested only when above 70 cm dbh. Approximately 20% of target species above minimum size for cutting are left as seed trees and future crop trees. During pre-harvesting inventory, trees selected for felling are cleared of all vines on or near the bole.

La Chonta uses a 'fishbone' harvesting strategy with a single primary north–south road bisecting each 850 ha block. Secondary roads and skid trails are then established and the location of these are guided by contour maps and the density of target trees as a guide. Secondary roads are generally 100–150 m apart and run in an east–west direction on either side of the primary road. Chainsaw teams trained in directional felling techniques try to reduce damage to the residual stand during logging. Removal and loading of boles is conducted using rubber-tired skidders to reduce soil compaction. It is intended that blocks be re-cut in 25–30 years.

2.3. Experimental design

We conducted vegetation structure and phenology surveys during June and July 2004 within 36 logging gaps and 36 natural tree-fall gaps in the unlogged forests of the La Chonta concession (Fig. 2). In the unlogged forest, gaps were restricted to treefalls greater than 50 cm dbh as this is the minimum cut diameter in the logged forest. Phenology surveys were conducted from February to March 2004. To reduce the effects
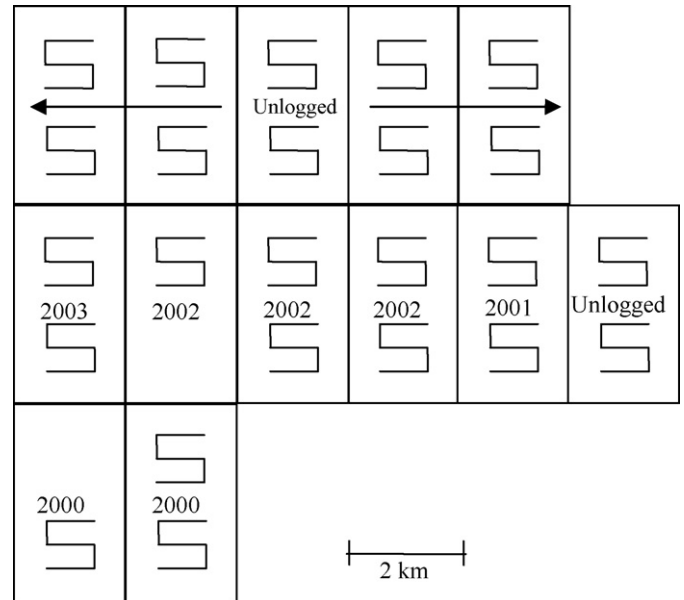

Fig. 2. Schematic diagram representing relative location of logging blocks (labelled with year of harvest) and unlogged sites used in this study within the subtropical humid forests of the La Chonta forestry concession, Santa Cruz, Bolivia. 'S' symbol represents transects cut within each block along which three gaps were located and sampled. Unlogged areas are to be harvested between 2004 and 2006.

of seasonal variation, logged and unlogged areas were surveyed on alternate days, as were blocks logged in different years. Sampling points were located at least 300 m apart.

2.4. Measurement of vegetation structure and floristics

At each gap, the size of the canopy opening (defined as a vertical hole in the forest extending through the canopy to within 2 m of the forest floor (Schemske and Brokaw, 1981)), was measured using the dimensions of the major axis and minor axis. Gap area was calculated using the formula for an ellipse. Within each gap, a 20 m × 20 m quadrat was marked. Within this, all trees, palms, poles, and stags were counted if part of their bole encroached on the quadrat. Poles were defined as trees less than 10 cm dbh but taller than 3 m. Stags were defined as dead trees greater than 10 cm dbh. Palms up to 3 m in height were counted. The numbers of fruiting and flowering plants were counted as part of the phenological assessment.

Three measurements of vegetation structure were taken from four equidistant markers located 7 m from the quadrat centre. To assess understorey density of vegetation, we used a 2 m rope held vertically, marked at 10 cm intervals. The rope was held in the centre of the quadrat with the number of bands visible from each of the four markers counted, thereby providing an index of understorey density. Canopy height was measured at each marker using a clinometer and a laser rangefinder. Canopy cover was quantified at each marker using a densiometer.

At each of the four markers, a 2 m × 2 m plot was defined. In each plot, we estimated the percentage cover of grasses, ferns, palms, seedlings, dead wood, dirt, rock, sand, *Erythrochiton fallax* Kallunki (Rutaceae), *Heliconia* spp. (Heliconiaceae),

other herbs, and vines. Vine coverage was divided into two classes: 0–1 m ("vine low") and 1–2 m above ground ("vine high").

2.5. Statistical analysis

We used Principal Components Analysis (PCA, Jolliffe, 2002) to reduce the data set to a smaller number of orthogonal axes that explained the variation in habitat structure in each of the gaps. Due to the low percentage of overall variation accounted for with the PCA, we used the conservative approach of interpreting only those eigenvalues belonging to the 'cliff' region of the scree plot (Cattell, 1966; Jackson, 1993). General linear regression (Timm and Mieczkowski, 1997) was used to determine whether treatment (logging gaps versus natural tree-fall gaps), or time since treatment, were related to axes, with predictions from the regression model indicative of convergence with or divergence from habitat categories in the unlogged forest.

3. Results

Twenty-two physiognomy and phenological variables were analysed using Principal Components Analysis (Table 1). The PCA extracted three components of variation from 22 variables which accounted for 41% of the variability in the data set. Principal component I accounted for 17% of the variance and

contrasted larger more open gaps with smaller gaps that contained a higher density and diversity of tree species. The vegetation parameters contrasted in PC I also distinguished logging gaps from natural tree-fall gaps. PC II accounted for a further 13% of the variability of the data set and contrasted gaps with a high percentage cover of vines, with gaps with a high percentage cover of seedlings. PC III accounted for a further 11% of the data set variability and contrasted gaps with a high cover of *Heliconia* spp. with those possessing bare ground.

Table 2 shows the means and standard errors for vegetation structure and phenology variables in natural gaps and gaps created by reduced-impact logging. Results from general linear regression demonstrated that logging gaps were significantly larger than natural gaps (d.f. 1, vr. 6.38, $p = 0.014$; Fig. 3) and were significantly lower in understorey density (d.f. 1, vr. 4.75, $p = 0.033$). The difference in understorey density was in part driven by reduced coverage of vines in logging gaps (d.f. 1, vr. 8.64, $p < 0.01$). Seedlings were more prevalent in logging gaps than in natural tree-fall gaps (d.f. 1, vr. 13.97, $p < .001$). Assessment using years since logging as a treatment variable demonstrated that the percentage cover for species of *Heliconia* was significantly higher in logging gaps than in natural gaps 2 years following logging (d.f. 4, vr. 3.05, $p = 0.023$) while flowering activity was significantly higher in logging gaps 3 years after logging (d.f. 4, vr. 3.71, $p < 0.01$). Canopy cover was significantly reduced in logging gaps for the first 2 years following logging (d.f. 4, vr. 4.34, $p < 0.01$), and leaf litter depth was significantly reduced in logging gaps for the first year following logging (d.f. 4, vr. 3.07, $p = 0.02$).

Table 1

Results of a Principal Components Analysis (PCA) of vegetation structure variables for logging and natural gaps ($n = 72$) in the subtropical humid forests of the La Chonta forestry concession, Santa Cruz, Bolvivia

	Logging gaps and natural tree-fall gaps		
PCA component	I	II	III
Eigenvalue	3.80	2.94	2.33
Cumulative % variance explained	17.28	30.65	41.25
Variable loadings			
No. of tree species/0.04 ha	0.40	−0.12	−0.10
Canopy openness	0.37	0.20	−0.10
No. of trees/0.04 ha	0.35	−0.14	0.01
Canopy height (m)	0.33	0.22	0.00
Canopy cover (%)	0.33	0.07	−0.03
No. of poles/0.04 ha	0.28	0.07	−0.24
Leaf litter depth	0.23	−0.26	0.24
Fern % cover	0.18	−0.04	0.34
Basal area sq. m/0.04 ha	0.17	0.15	−0.03
Leaf litter % cover	0.10	−0.25	0.22
Erythrochiton fallax % cover	0.10	0.10	−0.11
Palm % cover	0.07	0.03	0.17
No. of flower plants/0.04 ha	0.04	0.07	0.40
No. of fruiting plant/0.04 ha	0.03	−0.28	0.02
Seedling % cover	−0.01	0.28	−0.16
Understorey density (0–20)	−0.02	0.17	−0.08
No. of palms/0.04 ha	−0.03	0.00	0.26
Vine high % cover	−0.04	−0.46	−0.18
Bare ground % cover	−0.10	0.17	−0.30
Vine low % cover	−0.11	−0.46	−0.23
Heliconia spp. % cover	−0.12	0.16	0.48
Gap size (m²)	−0.31	0.18	−0.01

Results listed in descending order for principal component I (PC I).

Table 2

Mean scores for 22 variables relating to vegetation structure within natural and anthropogenic gaps in the reduced-impact logged area of the subtropical humid forests of the La Chonta forestry concession, Santa Cruz, Bolivia

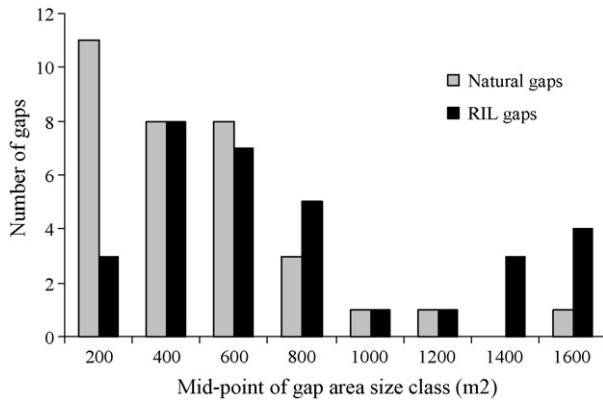|	Unlogged		Logged	
	Mean	S.E.	Mean	S.E.
No. of tree species/0.04 ha	8.4	0.5	7.7	0.5
No. of trees/0.04 ha	14	1	11.5	0.7
Canopy height (m)	9.8	0.8	11	0.8
Canopy cover (%)	91	1.1	88	1.5
No. of poles/0.04 ha	24.1	1.5	24.5	1.9
Leaf litter depth	2.1	0.1	1.9	0.1
Fern % cover	28.3	2.7	23.9	2.3
Basal area sq. m/0.04 ha	0.5	0.1	0.5	0.1
Leaf litter % cover	80	1.6	79	1.8
Erythrochiton fallax % cover	5	2.3	1	0.7
Palm % cover	1.4	0.5	2.2	0.6
No. of flower plants/0.04 ha	15.2	3	11.5	3
No. of fruiting plant/0.04 ha	1	0.3	0.4	0.1
Seedling % cover	13.3	1.7	23.6	2.2
Understorey density (0–20)	5.3	0.5	6.8	0.5
No. of palms/0.04 ha	0.7	0.5	1.1	0.8
Vine high % cover	10.7	2.1	3.8	1
Bare ground % cover	4.3	0.8	3.3	0.8
Vine low % cover	19.9	2.7	13.7	1.9
Heliconia spp. % cover	15	2.5	20	3.2
Gap size (m²)	404.5	52.4	638.2	76.9

S.E. stands for standard error.

Fig. 3. Distribution of gap sizes within the subtropical humid forests of the La Chonta forestry concession, Santa Cruz, Bolvivia.

4. Discussion

Anthropogenic gaps in the reduced-impact logged area of La Chonta were significantly larger than their naturally formed counterparts in the unlogged forests of the concession. The difference in size results from selective logging being an exogenous cause of mortality that targets the larger, healthy, and well-formed individuals of a forest's tree species (Auld and Bull, 2003), with mortality often resulting in the bole cutting a swathe through the surrounding canopy (Whitmore, 1978). Under natural conditions, the death of even the largest trees may have a relatively small impact on the surrounding canopy if mortality results in the slow deterioration of the standing tree (Howe, 1990). Inevitably these differences result in selective extraction increasing the frequency of large gaps permeating a forest canopy. In addition, the size of anthropogenic gaps in the La Chonta concession was further exacerbated by the targeting of the large free-standing fig *Ficus boliviana*. This species regularly achieves a dbh of >200 cm and possesses a disproportionately large crown often exceeding 30 m in diameter (A and A.M. Felton pers obs). In our study, felling of *F. boliviana* was responsible for the majority of gaps over 1000 m^2, including four that exceeded 1500 m^2.

Of concern to forest managers is the association between forest disturbance and liana infestation. Lianas depend on the physical support of other plants and their presence is known to inhibit tree regeneration, restrict the growth rates of tree seedlings, and reduce the economic value of commercial trees through an associated increase in stem deformation (Carse et al., 2000). Lianas generally increase in density after natural and anthropogenic forest disturbance (Hegarty and Caballé, 1991), and thrive in unmanaged timber operations (Pinard and Putz, 1994). Lianas are of special concern to managers of Bolivian tropical forests where some of the highest liana densities in the world have been found (Pérez-Salicrup et al., 2001). To reduce the economic cost of lianas, and to minimize "domino" tree-falls while harvesting, managers at La Chonta employ pre-harvest liana cutting which involves the cutting of lianas within a 30 m radius of the bole of target trees

approximately 1 year prior to logging (Alvira et al., 2004). As we found significantly fewer lianas in logging gaps than in natural tree-fall gaps, it appears that the technique of pre-harvest liana cutting is effective at reducing liana proliferation, at least over the 4 years subsequent to harvest. Our results concur with Gerwing and Uhl's (2002) study from the Brazilian Amazon, which also found that pre-logging liana cutting significantly reduced liana densities in logging gaps. Part of the reason for reducing liana density is to induce a concomitant increase in seedling density. As seedling densities were higher in logging gaps, our results suggest that liana reduction is helping to promote tree seedling regeneration. However, as the density of tree seedlings also can increase with both disturbance (Fredericksen and Mostacedo, 2000), and gap size (Orians, 1983), increased seedling densities in logging gaps may be the outcome of several factors. Although the increase in seedling regeneration is a positive result for forest managers, findings suggest that few of them are likely to belong to commercial species.

The larger a gap in the canopy, the further local microclimatic conditions can be altered, including (but not limited to) changes to the availability of photosynthetically active radiation, heat fluxes, wind, and humidity levels (Pinard and Cropper, 2000; Asner et al., 2004b). These microclimatic conditions are resource axes that can be competitively partitioned among colonizing plant species, with some species being favoured or disadvantaged at different points along the gap-size gradient (Denslow, 1980). In our study, members of the genus *Heliconia* had significantly higher densities in logging gaps, and thus appear to benefit from microclimatic conditions associated with decreased canopy cover and increased gap size. *Heliconia* is a large, primarily neotropical genus (200–250 spp.) of rhizomatous, herbaceous perennials. They are common occupants of areas characterized by high solar radiation (Rundel et al., 1998).

Higher levels of radiation are commonly associated with increased reproductive activity in understorey plants (Costa and Magnusson, 2003). We found that this pattern was most noticeably reiterated by the abundant flower production of *Heliconia* spp. in logging gaps 3 years after harvest. We observed two species of hummingbird (Reddish hermit *Phaethornis ruber* L. and White-chinned sapphire *Hylocharis cyanus* Vieillot) regularly visiting the flowers of both *Heliconia* spp. and *Costa* spp. in natural and anthropogenic gaps (A. Felton pers. obs.). The increased provision of nectar by these and other understorey plant species in logging gaps may go some way to offsetting the loss of alternative sources of food (e.g. epiphytes on felled trees) for nectarivores (Grieser Johns, 1997). Unfortunately, it is also possible that the rapid colonization of logging gaps by understorey herbaceous species such as *Heliconia* spp. may limit commercial tree species regeneration (Fredericksen and Mostacedo, 2000).

Insufficient regeneration of commercial tree species in Bolivian forestry concessions is of significant concern to forest managers and ecologists (Mostacedo and Fredericksen, 1999; Jackson et al., 2002). In the logging gaps of La Chonta,

regeneration is dominated by non-commercial pioneer species, at the expense of shade-tolerant commercially valuable species such as *Batocarpus amazonicus* Ducke, *Pseudolmedia laevis*, and *Ampelocera ruizii* Klotzsch (Park et al., 2005). Because pioneer species regenerate predominantly in larger gaps (Brokaw, 1985), some researchers have suggested the adoption of logging techniques that create smaller disturbances, thereby promoting the regeneration of shade-tolerant species (Park et al., 2005), and reducing the likelihood of pioneer invasion (Brokaw, 1985; Uhl et al., 1988). We suggest that although the size of logging gaps is an issue that needs to be addressed, problems with the regeneration of shade-tolerant species also may result from more fundamental differences between logging gaps and natural tree-fall gaps.

Studies in natural tree-fall gaps of unmanaged forests suggest that although the regeneration requirements of some tree species are adapted to different gap microenvironments, resultant gap partitioning by species under natural conditions is often overridden or blurred by stochastic events that can both limit partitioning and promote diversity in gaps (Brokaw and Scheiner, 1989; Brokaw and Busing, 2000). These authors contend that a principle stochastic driver of this diversity is pre-gap advanced regeneration. Juveniles of shade-tolerant species that are present prior to the formation of the gap, and survive gap formation, can dominate gap regrowth simply by being the tallest individuals at the time of disturbance (Brown and Jennings, 1998; Hubbell et al., 1999). In this way stochasticity acts as a ''keystone process'', promoting higher diversity in gaps by reducing the competitive advantage of a few individual pioneer species better adapted to microclimatic conditions in that particular gap.

In Bolivian forestry concessions, the reasons for recruitment failure of commercial tree species include insufficient seed trees, poor seed viability, high seed predation, and excessive interplant competition (Mostacedo and Fredericksen, 1999; Pariona et al., 2003). We suggest that in addition to these problems, logging gaps lack adequate regeneration of shade-tolerant commercial species because extensive disturbance of soils by skidders during bole removal (Jackson et al., 2002) causes the mortality of shade-tolerant species in advanced stages of regeneration achieved prior to gap formation. This removes the competitive height advantage needed by shade-tolerant species to compete within gaps, and emphasizes the advantage of pioneer species possessing faster growth rates within the favourable microclimatic conditions of large gaps (Brokaw, 1985). It is our view that this process is at least partly causes domination of logging gaps by regenerating pioneer species.

There are a number of repercussions for silviculture if this conclusion is proved to be correct. First, estimates of how small logging gaps have to be to avoid dominance by shade-intolerant species may be inaccurate if they are based solely on literature from studies of natural regeneration in tree-falls from unmanaged tropical forests. Second, the benefits of soil scarification, as a means of promoting the regeneration of certain species (e.g. *Schizolobium amazonicum*), need to be weighed against the increased risk of invasion by non-commercial pioneers. Studies of scarified logging gaps have found that subsequent regeneration was dominated by early successional tree species (Fredericksen and Pariona, 2002). Third, if stochasticity is acting as a keystone process that serves to promote tree species diversity, then weakening this process will be of concern to those trying to ensure silvicultural techniques maintain commercial tree species abundance in Bolivian forestry concessions.

4.1. Management implications

Our research suggests that pre-harvest liana cutting is successful at reducing liana density for at least several years after logging. This procedure also appears to be an effective means of increasing the percentage cover of tree seedlings in logging gaps. However, current silvicultural practices (specifically the harvesting of *Ficus boliviana*) are potentially negating the benefits of increased seedling density by creating large gaps with microclimatic conditions preferentially beneficial to the regeneration of non-commercial pioneer species. We propose that this problem can be further exacerbated through damage to shade-tolerant species in advanced stages of regeneration during tree felling and bole removal. We suggest that research is needed to quantify the damage caused to commercial tree species in advanced stages of regeneration from each component of the felling and bole removal process. If subsequent research confirms that these processes are aiding regeneration dominance by pioneer species, then forest managers may need to increase supervision and economic incentives for tree fellers and skidder operators to recognize and reduce damage to commercial tree species in advanced stages of regeneration. The more technically challenging solution of species-specific site preparation, and enrichment planting, may also be needed (Mostacedo and Fredericksen, 1999).

Regardless of the precise nature of the solution, the dominance of non-commercial pioneers in logging gaps (Park et al., 2005), lack of adequate regeneration for most commercial species (Pariona et al., 2003), and current projections of dramatic declines in the volume of future harvests (Dauber et al., 2005), all point to the unsustainability of current reduced-impact logging practices, and the need for reassessment of anthropogenic disturbance processes employed in these forests.

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